Pestic. Sci. 1997, **51**, 443–449

Comparative Testing of Several Juvenile Hormone Analogues in Two Species of Locusts, *Locusta migratoria migratorioides* and *Schistocerca gregaria*

M. Paul Pener,[1]* Amir Ayali,[1] Gal Kelmer,[1] Blanká Bennettová,[2] Václav Němec,[2] Martin Rejzek[3] & Zdeněk Wimmer[3]

[1] Department of Cell and Animal Biology, The Hebrew University of Jerusalem, Jerusalem 91904, Israel
[2] Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic
[3] Institute of Organic Chemistry and Biochemistry, Academy of Sciences of the Czech Republic, Flemingovo námesti 2, 166 10 Prague 6, Czech Republic

(Received 16 September 1996; revised version received 9 May 1997; accepted 2 July 1997)

Abstract: Effective treatment with juvenile hormone analogues (JHAs) of early penultimate or early last-instar locust hoppers induces a supernumerary 'extra' nymphal instar. These 'extra' nymphs, also termed 'adultoids', die in the course of, or shortly after, an 'extra' moult. Less effective treatment results in imperfect adults with crumpled twisted wings which presumably limit their flight and migratory abilities. Extremely effective treatment leads to death in the next moult. Comparing dose-response relations of (7*S*)-methoprene, fenoxycarb, pyriproxyfen and a new JHA, R70-1 (ethyl *cis*-*N*-{2-[4-(2-hydroxycyclohept-1-ylmethyl)phenoxy]ethyl}carbamate), we revealed that route of administration, instar of the recipient hopper, and species may alter over 1000-fold the ED_{50} for the same JHA. *Locusta migratoria migratorioides* is much more susceptible to JHAs than *Schistocerca gregaria*. The lowest ED_{50} found to induce adultoids and subsequent death in the 'extra' moult was 0·12 μg pyriproxyfen injected in olive oil to early penultimate instar hoppers of *L. m. migratorioides* (about 0·5 μg g^{-1} fresh weight). R70-1 was more active than pyriproxyfen following the more practical topical application to early last-instar hoppers of *L. m. migratorioides*, 5·9 μg and 46 μg per hopper, respectively (about 10 μg g^{-1} and 78 μg g^{-1} fresh weight). The high susceptibility of last-instar *L. m. migratorioides* nymphs to topically applied R70-1 is promising from the practical standpoint.

Pestic. Sci., **51**, 443–449, 1997
No. of Figures: 3. No. of Tables: 2. No. of Refs: 25

Key words: juvenile hormone analogues, methoprene, fenoxycarb, pyriproxyfen, *Locusta migratoria*, *Schistocerca gregaria*

1 INTRODUCTION

Interference with the endocrine system of insects has long been considered as a sound approach to development of bio-rational pest management. Major applied success has been achieved by disturbing metamorphosis with juvenile hormone analogs (JHAs). In the 1970s, methoprene (ZR 515, 'Altosid') and hydroprene (ZR 512, 'Altozar') were the first JHAs to be used as commercial non-conventional insecticides.[1]

Methoprene and some other early JHAs, as well as exogenous juvenile hormones (JHs), affect acridids, but effective doses to induce JH-controlled physiological effects, or disturb metamorphosis, are very high, hundreds or at least tens of micrograms per insect.[2–6]

* To whom correspondence should be addressed.
Contract grant sponsor: Hebrew University of Jerusalem.

 Pestic. Sci. 0031-613X/97/$17.50. Printed in Great Britain

In the 1980s further potent JHAs, such as fenoxycarb (Ro 13-5223, 'Insegar') and pyriproxyfen (S-31183, 'Sumilarv') were developed.[7] Effective doses of fenoxycarb on acridids[8,9] were rather similar to those of the former JHAs, but experiments aimed primarily to investigate various JH-dependent physiological processes in acridids revealed that pyriproxyfen is effective in doses of a few micrograms per insect.[5,10,11]

In the present study we compared the lethal consequences of the morphogenesis-disturbing (= metathetely-inducing) effect of methoprene, fenoxycarb, pyriproxyfen and a new JHA, R70-1, ethyl *cis-N*-{2-[4-(2-hydroxycyclohept-1-ylmethyl)phenoxy]ethyl} carbamate, compound **24** of Rejzek *et al.*[12] These JHAs were tested by various routes of administration to early IVth or early Vth-instar hoppers of the African migratory locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire) and the desert locust, *Schistocerca gregaria* (Forskål).

2 MATERIALS AND METHODS

2.1 Insects

Crowded *L. m. migratorioides* and *S. gregaria* from the Jerusalem stock cultures[13,14] were used. Experimental locusts were kept in 12-litre metal cages, 7–20 locusts per cage, under a 12 : 12 h light : dark regime, 38(±1)°C during the photophase and 27(±1)°C during the scotophase. Both species of locusts were fed on Kikuyu grass (*Pennisetum clandestinum* Hochst), freshly supplied daily, and flaked oats. This diet was supplemented with cabbage for *S. gregaria.*

2.2 Juvenile hormone analogues (JHAs) and their mode of administration

The (7*S*)-methoprene used was a gift from Dr G. B. Staal of Sandoz Crop Protection (formerly Zoecon Research Laboratories), Palo Alto, California. Fenoxycarb and pyriproxyfen were gifts from Dr R. Maag Ltd, Switzerland and Sumitomo Chemical Co. Ltd, Japan, respectively. R70-1, was synthesized in the Institute of Organic Chemistry and Biochemistry of the Academy of Sciences of the Czech Republic, Prague. These JHAs were administered routinely by the following routes: (1) dissolved in acetone and topically applied in 4 or 5 μl of solvent to the dorsal side of the abdomen of each hopper; (2) dissolved in pure olive oil (Sigma) and injected in 4 or 5 μl of oil per hopper; (3) dissolved in acetone and injected in 1 μl of this solvent. In a few instances pure (7*S*)-methoprene without solvent was injected. We decided to employ injection in olive oil in some experiments after discovering that this route of administration can be more effective than topical application by about three orders of magnitude. Although not a practical method for pest control, such injections in oil throw light on the relative inefficiency of topical application. Injection in acetone was employed as an alternative direct delivery of the JHAs into the insects for comparison with injection in oil. The JHAs were applied topically or injected into early IVth-(penultimate)-instar hoppers 0–28 h after the moult, or to early Vth-(last)-instar hoppers 0–18 h after the moult.

We pursued treatments of early penultimate-instar hoppers to explore the possibility of extending the time-window of susceptibility to JHA; usually, this time window is limited to early last-instar nymphs in hemimetabolous insects.

2.3 Evaluation of results

Usually, the metamorphosis-inhibiting effect of JH or JHAs is evaluated by lengthy descriptions of the larval-adult intermediates or by a rather arbitrary ID_{50} ('inhibition dose'), defined as the dose producing creatures that exhibit 50% of juvenile characters.[15] Another method, using ED_{50} ('effective dose'), or EC_{50} ('effective concentration'), is based on some taxon-dependent, easily recognizable morphological or physiological characteristic, or on a 'minimum discernible effect,' induced by exogenous JH or JHA.[15] It was observed in previous studies,[4] as in the present work, that effective treatment of locust hoppers with exogenous JH or JHA induces a supernumerary nymph in the VIth instar (which is the adult instar in the course of normal development). These creatures, also termed 'adultoids',[3] because they are not perfect nymphs, invariably die in an extra moult (from the VIth to the VIIth instar), or shortly after the extra moult, being unable to shed, or shed completely, the exuviae. This mortality, considered as a 'physiological death,' was selected as the response on which the dose-response data are based. In other words, the ED_{50} is the dose that induces death in a supernumerary moult from the VIth to the VIIth instar in 50% of the locusts treated, and it is practically the LD_{50} (lethal dose 50%) for a delayed mortality. Only adultoids with prominent nymphal characteristics exhibited this supernumerary moult, which usually occurred 10–14 days after the moult to the VIth instar, though in a few adultoids it was delayed up to a maximum of 24 days. The dose-response data were submitted to probit analysis, using POLO-PC program,[16–18] and the ED_{50}, as well as data for plotting the regression line (log dose—% of response) on probit scale were obtained. These ED_{50} values, as defined above, are several times higher than the somewhat arbitrary ID_{50} ('inhibition dose' 50%, see above) values and the latter are still higher than the 'minimum discernible effect' which is adults with curled-crumpled

wings in acridids. In a few instances we also observed that very high doses cause death in the next or second-next moult after treatment, that is from the IVth to the Vth or from the Vth to the VI instar, before or at the overt appearance of the extra nymphal (=adultoid) instar (see Section 3).

3 RESULTS

Table 1 shows the values of ED_{50} obtained, or, in the cases of ineffective or less effective treatments (=no, or less than 50%, VIth-instar adultoids and consequently no, or less than 50%, death in the 'extra' moult), the maximum dose administered. Full dose-response data are presented graphically only for effective topical applications, or for special comparison of different routes of administration of the same compound.

Injection of pyriproxyfen in olive oil to IVth-instar *L. m. migratorioides* hoppers was exceptionally effective (Fig. 1, line A), yielding an ED_{50} value as low as 0·12 μg per hopper (about 0·5 μg g^{-1} fresh weight), lower by about three orders of magnitude than the ED_{50} values obtained by other routes of administration of the same compound to conspecific hoppers in the same instar (Fig. 1, lines B and C; see also Table 1). The extremely high susceptibility of these hoppers to the pyriproxyfen injected in oil cannot be explained by direct delivery of the compound into the body, because the same compound injected in acetone into similar hoppers was less effective by almost 1000 times (compare line A to line C in Fig. 1). Fourth-instar hoppers of *S. gregaria* were over 800 times less susceptible than *L. m. migratorioides* to pyriproxyfen injected in oil and such hoppers of *S. gregaria* were even less susceptible to pyriproxyfen by other routes of administration (see Table 1).

Fenoxycarb topically applied to IVth-instar hoppers of *L. m. migratorioides* was moderately effective (Fig. 2). Methoprene administered to conspecific similar hoppers was rather ineffective by topical application, but it was effective by injection in olive oil (Table 1). Fourth-instar hoppers of *S. gregaria* were practically not susceptible to fenoxycarb, or to topically applied methoprene, and showed very low susceptibility even to methoprene injected in olive oil or without solvent (Table 1).

As already mentioned (Section 2.3), mortality in the moult from the IVth to the Vth, or from the Vth to the VIth instar was induced by doses higher than those producing VIth-instar adultoids and subsequent death

TABLE 1

Effective Dose (ED_{50}) to Induce 50% Supernumerary (VIth-Instar) Nymphs and Subsequent Death in (or shortly after) an 'Extra' Moult, from the VIth to the VIIth Instar, in *Locusta migratoria migratorioides* and *Schistocerca gregaria* following Treatment of Early IVth-(penultimate)- or Early Vth-(Last)-Instar Nymphs with Juvenile Hormone Analogues (JHA) Administered by Various Routes

				Locusta		Schistocerca	
Nymphal instar treated	*JHA*[a]	*Administered by*	*Dissolved in*	*ED_{50} (μg)*	*Effect at maximum dose (%)*[b]	*ED_{50} (μg)*	*Effect at maximum dose (%)*[b]
IV	P	Injection	4 or 5 μl olive oil	0·12		103[e]	
IV	P	Injection	1 μl acetone	108[c]		>500	23·5
IV	P	Topical application	4 or 5 μl acetone	135		>2000	16·7
IV	F	Injection	4 or 5 μl olive oil	>150[d]	0·0[d]	>150[d]	0·0[d]
IV	F	Topical application	4 or 5 μl acetone	108[e]		>2000	0·0[g]
IV	M	Injection	4 or 5 μl olive oil	31		>2000	22·2
IV	M	Injection	Without solvent	No test		>2000	28·6
IV	M	Topical application	4 or 5 μl acetone	>1000	12·9	>2000	0·0
V	P	Topical application	5 μl acetone	46		124	
V	R70-1	Topical application	5 μl acetone	5·9		~200[f]	

[a] JHAs: P-pyriproxyfen, F-fenoxycarb, M = (7*S*)-methoprene, R70-1 = compound no. **24** of Rejzek *et al.*[12]

[b] Percentage of supernumerary nymphs and subsequent death in an 'extra moult' obtained with the maximum dose (less than the ED_{50}) shown in the preceding column.

[c] There was mortality also in the moult from the Vth to the VIth and from the IVth to the Vth instar (see Table 2). The ED_{50} presents cumulative death in the moult from the Vth to the VIth instar and in the 'extra' moult.

[d] No doses higher than 150 μg were employed because the limit of solubility of fenoxycarb in olive oil is about 30 μg μl^{-1}. This dose did not cause 'extra' moult, though it induced moderate or slight inhibition of adult morphogenesis in *L. m. migratorioides* and *S. gregaria*, respectively.

[e] Higher doses induced some mortality also in the moult from the Vth to the VIth instar.

[f] Approximate figure, based on two doses only; 50 and 200 μg per hopper, yielding 0% and 42% mortality in 'extra' moult, respectively.

[g] Moderate inhibition of adult morphogenesis but no 'extra' moult.

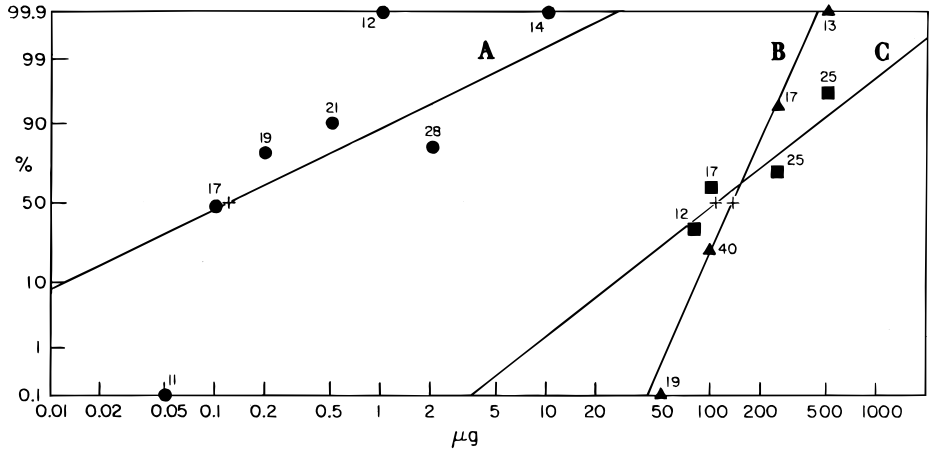

Fig. 1. Probit lines for effective dose (to induce mortality in an 'extra' moult, or in the moult from the Vth to the VIth instar) of pyriproxyfen administered by various routes to 0–28-h-old IVth-instar hoppers of *Locusta migratoria migratorioides*. Line A (●) injection in 4 or 5 μl olive oil; line B (▲) topical application; line C (■) injection in 1 μl acetone. Abscissa: dose in μg (note logarithmic scale); ordinate: probit in % values. Numbers at data points show *n.* + marks ED_{50} values.

in an 'extra' moult. However, this response was also much affected by the mode of administration. Following injection of pyriproxyfen in acetone to early IVth-instar *L. m. migratorioides* hoppers, doses close to the ED_{50} already caused some mortality in these earlier moults (Table 2; for ED_{50} see Table 1). In contrast, following injection of pyriproxyfen in olive oil into similar hoppers, the dose of 50 μg per hopper, over 400 times higher than the ED_{50}, induced only 0% and 25% mortality in the moult from the IVth to the Vth and from the Vth to the VIth instar, respectively. Relatively high doses of fenoxycarb (500 or 1000 μg per hopper) topically applied to IVth-instar *L. m. migratorioides* and of pyriproxyfen (250 or 500 μg per hopper) injected in olive oil into IVth-instar *S. gregaria* also caused some death in these early moults (see footnote '*e*' in Table 1). In all instances, further increase of the high doses shifted the mortality from later to earlier moults (Table 2).

Early Vth-instar *L. m. migratorioides* nymphs were highly susceptible to topically applied R70-1 (Fig. 3, line A); the ED_{50} was 5·9 μg per hopper (about 10 μg per g fresh weight). This value was about eight times lower than the ED_{50}, 46 μg per hopper, obtained for topical application of pyriproxyfen to similar nymphs (Fig. 3, line B). The latter, however, was over three times lower than the ED_{50} (135 μg per hopper, see Fig. 1, line B) for pyriproxyfen topically applied to IVth-instar *L. m. migratorioides* nymphs. *S. gregaria* again turned out to be less susceptible than *L. m. migratorioides*. The ED_{50} obtained for early Vth-instar *S. gregaria* nymphs was 124 μg and about 200 μg per hopper (preliminary figure, see footnote '*f*' in Table 1) following topical application of pyriproxyfen and R70-1, respectively. Interestingly, *S. gregaria* was more susceptible to pyriproxyfen than to R70-1, but an opposite situation obtained in *L. m. migratorioides*. Another interesting finding is that the POLO-PC program did not show

TABLE 2

Mortality in Moult Caused by Injection of Pyriproxyfen in 1 μl of Acetone into 0–28-h-old IVth-(Penultimate)-Instar Hoppers of *Locusta migratoria migratorioides*. Numbers show number of locusts, except in the column for the dose

Dose injected in μg	*N*	*Mortality in moult*			*VI*[a] *permanent*	*Lost*[b] *in*	
		IV–V[a]	*V–VI*[a]	*VI–VII*[a]		*V*[a]	*VI*[a]
500	59	25	24	0	1	9	0
250	39	2	9	8	8	1	11
100	20	0	1	10	7	0	2
80	17	0	0	4	8	0	5

[a] Roman numerals represent the number of the instar. In the course of normal development the VIth instar is the adult. Two Roman numerals separated by a hyphen in the columns of mortality show the moult from a given instar (first Roman numeral) to the next one (second Roman numeral).

[b] Escaped, died accidentally, or died not in moult.

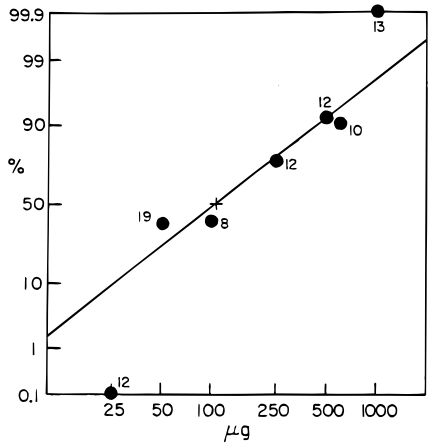

Fig. 2. Probit line for effective dose (to induce mortality in an 'extra' moult) of fenoxycarb topically applied to 0–28-h-old IVth-instar hoppers of *Locusta migratoria migratorioides*. Abscissa, ordinate, marking of *n* and of ED_{50} as in Fig. 1.

statistically significant differences in the slopes of the three lines in Fig. 3. Therefore, these lines may be considered as parallel for treatment of Vth-instar nymphs by topical application, irrespective of the species and the kind of JHA.

In locusts, the metamorphosis-inhibiting 'minimum discernible effect' (MDE) of JH or JHAs on morphogenesis (Section 2.3) is curled-crumpled wings in the adults obtained from the treated hoppers. We did not make a methodical dose-response study in relation to this MDE. Nevertheless, testing very low doses, we observed that, in some instances, doses lower by about an order of magnitude than the ED_{50} (as defined in the present study) are capable of inducing the MDE. Thus, for example, in *L. m. migratorioides*, topical application of 10 μg of pyriproxyfen to IVth-instar hoppers (ED_{50} = 135 μg, Table 1; ED_{50}/MDE = 13·5), or of

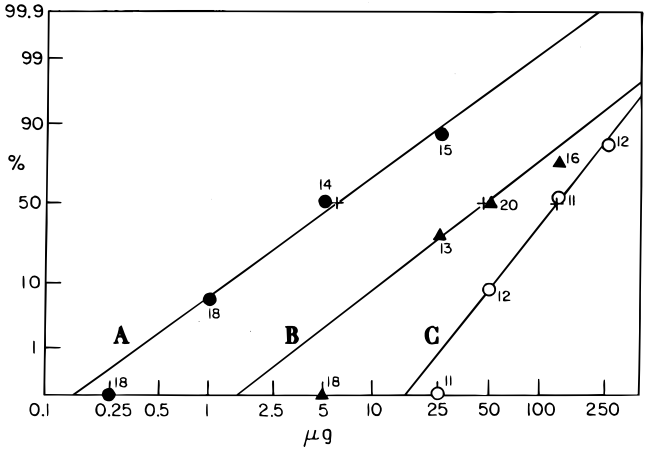

Fig. 3. Probit line for effective dose (to induce VIth-instar adultoids and mortality in an 'extra' moult) of some JHAs topically applied to 0–18-h-old Vth-instar locust hoppers. Line A (●) R70-1 applied to *Locusta migratoria migratorioides;* line B (▲) pyriproxyfen applied to *L. m. migratorioides;* line C (○) pyriproxyfen applied to *Schistocerca gregaria.* Abscissa, ordinate, marking of *n* and of ED_{50} as in Fig. 1.

5 μg of pyriproxyfen to Vth-instar hoppers (ED_{50} = 46 μg; ED_{50}/MDE = 9·2), or of 0·5 μg of R70-1 to Vth-instar hoppers (ED_{50} = 5·9 μg; ED_{50}/MDE = 11·8) induced wing deformations in the subsequent adults. In *S. gregaria* injection of 25 μg of pyriproxyfen in olive oil to IVth-instar hoppers (ED_{50} = 103 μg; ED_{50}/MDE = 4·1) resulted in the same.

All effective treatments and often treatments not resulting in morphogenetic effects induced green colour in the next and frequently also in the subsequent instar(s) (results are not shown), as expected in accord with the well known green-colour-inducing activity of JH or JHAs.[19]

4 DISCUSSION

The present study demonstrates that pyriproxyfen injected in olive oil into early IVth-instar hoppers of *L. m. migratorioides* is about 1000-fold more effective than the same compound administered by other routes to similar hoppers. The effectiveness of exogenous JHs or JHAs in insects has long been known to be influenced by the mode of administration.[15,20,21] Injection in oil was usually more effective than topical application in locusts,[10,13,14] but a 1000-fold difference in the susceptibility between these two methods was not recorded. As already mentioned, direct delivery of the pyriproxyfen into the body of the hoppers cannot explain the extreme effectiveness of the injection in oil, because the same compound injected in acetone was about 1000 times less effective.

It is repeatedly claimed and/or discussed in the literature that the oil droplet may serve as a depot which slowly releases JH-active compounds, preventing their rapid inactivation.[15,21–23] Such a 'slow release' of the pyriproxyfen from the oil may well be responsible for the present results. However, the extremely high susceptibility to pyriproxyfen injected in olive oil may be specific to early IVth-instar nymphs, because, in early Vth-instar nymphs of *L. m. migratorioides*, injection of this compound in oil seems to be only a few times more effective than its topical application.[10] Undoubtedly, further studies are needed to clarify the mechanisms underlying our findings.

The mode of administration also affected the response of the IVth-instar nymphs to methoprene, but the differences between injection in olive oil and topical application in acetone were less dramatic than in the case of the pyriproxyfen.

Injection of JHAs is obviously not a practical method for locust management. Nevertheless, the present findings are important because they clearly demonstrate that, under favourable circumstances, minute amounts of an effective JHA are capable of disturbing metamorphosis and even well-established methods of administration may waste over 99·9% of the JHA.

The present results show that pyriproxyfen is more effective than methoprene for disturbing metamorphosis following administration to IVth-instar *L. m. migratorioides* and *S. gregaria*. Other authors comparing non-metamorphosis-related effects also reported that pyriproxyfen is more effective than methoprene to induce green colour,[5] or vitellogenin synthesis[11] in *L. migratoria*.

Fenoxycarb topically applied to IVth-instar hoppers was effective in *L. m. migratorioides* but only very slightly so in *S. gregaria*. Bowers and Ortego[8] found that *S. americana* is susceptible to topically applied fenoxycarb, but they used Vth-instar nymphs as recipients. Indeed, in an earlier study,[24] Vth-instar nymphs of *S. gregaria* were observed to be more susceptible than conspecific IVth-instar nymphs to topically applied fenoxycarb. The effective doses of fenoxycarb topically applied to IVth- and Vth-instar nymphs of the grasshoppers, *Melanoplus sanguinipes* (F.) and *M. differentialis* (Thomas)[9] were comparable to those found in the present study.

Evaluation of the potencies of JHAs for practical pest management is often based on data obtained by topical application. It is important, therefore, that R70-1 showed the best effect following topical application to early Vth-instar nymphs of *L. m. migratorioides*, though it was not as effective as indicated by Rejzek *et al.*[12] However, the definition of the effective dose in the present study is based on a much more severe effect (supernumerary nymph and death in an 'extra' moult) than the ID ('inhibition dose') used by Rejzek *et al.*[12] Although Vth-instar nymphs of *S. gregaria* were much less susceptible to R70-1 than similar nymphs of *L. m. migratorioides*, the results obtained with the latter justify exploration of susceptibility to this compound in IVth-instar hoppers, as well as in other locusts and grasshoppers. It may be added that in locusts even the 'minimum discernible effect' (Section 2.3), which is adults with curled-crumpled wings, has practical importance because wing deformation may interfere with flight and prevent migration. We observed that doses lower by about one order of magnitude than the ED_{50} as defined in the present study are sufficient to induce wing deformation, though the exact ratio of the doses may depend again on compound, instar, species and mode of administration.

In all the cases tested, hoppers of *S. gregaria* were much less susceptible to JHAs than similar hoppers of *L. m. migratorioides*. The latter species is primarily graminivorous, whereas the spectrum of the natural diet of the former is much wider and includes also desert shrubs and trees.[25] It is feasible to assume, therefore, that *S. gregaria* is better equipped to inactivate secondary plant substances, i.e. chemical defences of the plants, and its lower susceptibility to JHAs perhaps reflects this ability.

The results demonstrate the great differences in susceptibility shown by different instars of the same species and by the same instar of different species. Therefore, each species and each instar should be tested for assessing reliably the effectiveness of a given JHA. The relatively low effective doses of topically applied R70-1 against Vth-instar nymphs of *L. m. migratorioides* are encouraging from the practical standpoint, but further research is needed for developing JHAs to a useful component of integrated locust pest management. Presumably, this prediction may be extended to other species of locusts, as well as to harmful grasshoppers.

ACKNOWLEDGEMENTS

This research was supported by an intra-mural grant for basic research from the Hebrew University of Jerusalem. We sincerely thank Dr H. Pener for probit analysis and appreciate Mr H. Abu-Hilal's help in maintaining the locust colonies. The gifts of (7*S*)-methoprene, fenoxycarb and pyriproxyfen, from Dr G. B. Staal (Sandoz Crop Protection), Dr Maag Ltd, and Sumitomo Chemical Co., Ltd, respectively, are gratefully acknowledged.

REFERENCES

1. Staal, G. B., Insect growth regulators with juvenile hormone activity. *Ann. Rev. Entomol.*, **20** (1975) 417–60.
2. Němec, V., Jarolim, V., Hejno, K. & Šorm, F., Natural and synthetic materials with insect hormone activity 7. Juvenile activity of the farnesane-type compounds on *Locusta migratoria* L. and *Schistocerca gregaria* (Forsk). *Life Sci.*, **9**, II (1970) 821–31.
3. Joly, P. & Meyer, A. S., Action de l'hormone juvénile sur *Locusta migratoria* (Orthoptère) en phase grégaire. *Arch. Zool. Exp. Gén.*, **111** (1970) 51–63.
4. Roussel, J.-P. & Perron, J.-M., Action de substances mimétiques de l'hormone juvénile sur *Schistocerca gregaria* Forsk. *Arch. Zool. Exp. Gén.*, **115** (1974) 251–62.
5. Hasegawa, E. & Tanaka, S., Genetic control of albinism and the role of juvenile hormone in pigmentation in *Locusta migratoria* (Orthoptera, Acrididae). *Jap. J. Entomol.*, **62** (1994) 315–24.
6. Fagoonee, I., Application of a juvenile hormone analogue on the desert locust *Schistocerca gregaria* Forskål by different techniques. *Ann. Zool. Ecol. Anim.*, **11** (1979) 185–94.
7. Henrick, C. A., Juvenoids and anti-juvenile hormone agents: past and present. In *Insect Chemical Ecology*, ed. I. Hrdý. Academia, Prague and SPB Acad. Publ., The Hague, 1991, pp. 429–52.
8. Bowers, W. S. & Ortego, F., Evaluation of juvenoid insect growth regulators on *Schistocerca americana*. *Insect Sci. Appl.*, **12** (1991) 71–5.
9. Capinera, J. L., Epsky, N. D. & Turick, L. L., Responses of *Melanoplus sanguinipes* and *M. differentialis* (Orthoptera: Acrididae) to fenoxycarb. *J. Econ. Entomol.*, **84** (1991) 1163–8.
10. De Kort, C. A. D. & Koopmanschap, A. B., A juvenile hormone analogue affects the protein pattern of the hae-

molymph in last-instar larvae of *Locusta migratoria*. *J. Insect Physiol*., **37** (1991) 87–93.
11. Edwards, G. C., Braun, R. P. & Wyatt, G. R., Induction of vitellogenin synthesis in *Locusta migratoria* by the juvenile hormone analog, pyriproxyfen. *J. Insect Physiol*., **39** (1993) 609–14.
12. Rejzek, M., Wimmer, Z., Šaman, D., Ričánková, M. & Němec, V., Synthesis and structure-activity relationships of juvenoids derived from 2-(4-hydroxybenzyl)cycloalkan-1-ones. *Helv. Chim. Acta*, **77** (1994) 1241–55.
13. Lazaroviçi, P. & Pener, M. P., Juvenile hormones (JHs) and completion of oöcyte development in the African migratory locust: A comparative and quantitative study. *Gen. Comp. Endocrinol*., **33** (1977) 434–52.
14. Pener, M. P. & Lazaroviçi, P., Effect of exogenous juvenile hormones on mating behaviour and yellow colour in allatectomized adult male desert locusts. *Physiol. Entomol*., **4** (1979) 251–61.
15. Sláma, K., Pharmacology of insect juvenile hormones. In *Comprehensive Insect Physiology Biochemistry and Pharmacology*, Vol. 11, *Pharmacology*, ed. G. A. Kerkut & L. I. Gilbert. Pergamon Press, Oxford, 1985, pp. 357–94.
16. Russell, R. M., Robertson, J. L. & Savin, M. E., POLO: A new computer program for probit analysis. *Bull. Entomol. Soc. Amer*., **23** (1977) 209–13.
17. Anonymous, *POLO-PC User's Guide to Probit or Logit Analysis*. LeOra Software, 1119 Shattuck Ave, Berkeley, California, 94707, Copyright 1987, 22 pp.
18. Robertson, J. L. & Preisler, H. K., *Pesticide Bioassays with Arthropods*. CRC Press, Boca Raton, Florida, 1992, 127 pp.
19. Pener, M. P., Locust phase polymorphism and its endocrine relations. *Adv. Insect Physiol*., **23** (1991) 1–79.
20. Wigglesworth, V. B., Chemical structure and juvenile hormone activity: Comparative tests on *Rhodnius prolixus*. *J. Insect Physiol*., **15** (1969) 73–94.
21. Sláma, K., Romaňuk, M. & Šorm, F., *Insect Hormones and Bioanalogues*. Springer-Verlag, Wien, 1974, 477 pp.
22. Wigglesworth, V. B., The hormonal regulation of growth and reproduction in insects. *Adv. Insect Physiol*., **2** (1964) 247–336.
23. Erley, D., Southard, S. & Emmerich, H., Excretion of juvenile hormone and its metabolites in the locust, *Locusta migratoria*. *J. Insect Physiol*., **21** (1975) 61–70.
24. Abdel-Hamid, M., Zaki, G. & Harb, M., Morphogenetic effects of fenoxycarb on late nymphal instars of the desert locust, *Schistocerca gregaria* Forsk. *Agric. Res. Rev*., **64** (1986) 103–7.
25. Uvarov, B., *Grasshoppers and Locusts*, Vol. 2. Centre for Overseas Pest Research, London, 1977, 613 pp.